VOLUME LXXIV NUMBER 1

THE
BOTANICAL GAZETTE

September 1922

DEVELOPMENT OF PLANT COMMUNITIES OF A SAND RIDGE REGION IN MICHIGAN

W. G. WATERMAN

(WITH TWELVE FIGURES)

Plant synecology is the study of the relations of plant communities to their environment. The subject may be divided into three major sections.

1. *Morphological and physiological synecology.*—The physiognomy, ecological structure, and floristic composition of plant communities and their relationship to the factors of the environment. This includes not merely an enumeration of the species and ecological forms present, but also the sociological value of the different members of the community, as suggested in the following topics: abundance, dominance, affiliation, genetic importance, constancy, etc.

2. *Geographic synecology.*—The distribution of plant communities, with special reference to the influence of the factors of environment.

3. *Genetic or dynamic synecology.*—The study of the development of plant communities on unit areas as the result of the action of biotic factors, modified by physiographic influences and by changes of climate.

In the early days of ecology, the distributional phase of synecology was more evident and was followed with almost no suggestion

of the others. In recent years the other phases have been increasingly studied, but all have generally been combined in a more or less haphazard fashion. In a geographically extended treatment of the subject, the distributional (geographic) division may either precede or follow the developmental (genetic) division. If the communities are considered merely from the standpoint of their floristic content, their distribution may be studied first, and this has been the historical order. Plant geography has been studied with increasing interest since the days of VON HUMBOLDT, and it is still an important branch of synecology. It is evident, however, that the distribution of communities identified and named in accordance with their position in a developmental series (associations, formations, etc.) cannot be carried out adequately until a genetical study of those communities has been completed. In a limited area the study of the distribution of communities is correspondingly limited, and is of value only as it helps to determine the developmental relationships of these communities.

As genetic synecology is the most recent branch of the subject, and its content is not yet fully organized, a brief historical statement will be in order at this point. COWLES (3) was the first to form a comprehensive system based on the dynamic element in plant communities, as a result of his difficulty in classifying the communities of the Chicago region in accordance with WARMING'S principles. He was so strongly impressed with the influence of the physiographic factors that he outlined his system on that basis. Later (4) he recognized climatic, physiographic, and biotic factors as the three great causes of plant succession.

CLEMENTS (1) pointed out that climatic and physiographic causes produce succession but not true development, that is, the building up of a quasi-organism; and that this was possible only by the action of biotic factors, and especially by the influence of the plants which compose the different communities. CLEMENTS bases his main divisions on his climaxes or "formations," his next division is into primary and secondary successions, and his third into hydrosere and xerosere, based on the water content of the initial area. For these divisions he also uses as adjective modifiers the term hydrarch and xerarch, suggested by COOPER (2). As these

latter refer especially to the beginning of the succession, they are more suitable in this connection than such terms as hydrosere, etc., which apply to the moisture content of the whole succession, because in most cases the initial moisture condition does not persist, and the substratum generally approaches a mesophytic condition. While this classification may be logically defensible, CLEMENTS does not give sufficient consideration to the fact that the actual lines of development are determined by the nature of the substratum, that the floristic content of the pioneer stages is absolutely different in clay, sand, or rock, and that it is only as the seres approach the climax stage that they begin to converge and to resemble each other. Furthermore, standing water should be regarded as a type of substratum, because its pioneer stages are practically identical in ponds on rock, sand, or clay, and are quite different from the pioneer stages of wet sand or clay, to which stages the term hydrarch should be restricted. The subdivisions of the primary succession (prisere), therefore, should be sand succession (psammosere), clay succession (geosere), rock succession (lithosere), and aquatic succession (hydrosere). The first three successions have wet and dry initial stages (hydrarch, xerarch). It is evident that this classification does not distinguish the many types of substratum containing mixed sand, clay, and gravel. It does not seem, however, that these are sufficiently well marked or sufficiently different as to vegetation to warrant establishing one or more additional seres for them at present.

The terminology of the units of genetic synecology is being much discussed at present. It is generally agreed that the fundamental unit in the developmental classification of communities is the association. At first this was defined in terms of the habitat, but in 1921 NICHOLS (7), as a result of several questionnaires sent to eighty-five ecologists, reported at the recent meeting of the Ecological Society of America at Toronto that a large majority of the ecologists consulted favored the following statements: (1) That the term plant association be recognized as applicable both to the abstract vegetation concept and to the concrete individual pieces of vegetation upon which this concept is based; (2) that plant association in the abstract be defined somewhat as follows: an ecological vegetation-

unit characterized by an essentially definite physiognomy and ecological structure, and by an essentially definite floristic composition as regards dominant species; (3) that plant association in the concrete be defined somewhat as follows: a plant community of essentially uniform (or homogeneous) physiognomy and ecological structure and of essentially uniform (or homogeneous) floristic composition as regards dominant species. This simply formulates the more or less unconscious practice of most ecologists, who, when speaking of "a *Scirpus-Typha* association" have a concrete community in mind, while "the *Scirpus-Typha* association" of a certain region is plainly an abstract concept.

The next higher unit is also generally recognized as the formation, but there is not yet the same agreement in regard to its content as there seems to be for the association. The following brief survey of the progress of opinion in regard to the formation is summarized from TANSLEY (9). According to the definition adopted by the Brussels Congress, the formation is composed of associations which differ in their floristic composition, but are in agreement (1) with the conditions of the habitat, and (2) as regards their growth forms. TANSLEY says, "Though this concept is apparently accepted by most European phytogeographers, it has little real hold on actual concrete research because it is abstract and one sided." In 1907 MOSS (5) proposed a unit, later embodied by TANSLEY (8), in which all associations developed on the same habitat or on one of essentially constant character were considered as belonging to one formation. Not all the stages of a succession were necessarily included in one formation. If the habitat obviously changed its character completely, it was recognized that a new formation had been initiated. This conception was widely criticized, and TANSLEY admitted the validity of criticisms of the habitat element in the definition. CLEMENTS (1) refused to recognize any formations except those determined by climate, regarding all communities in a region where forests are climatically possible only as stages in the development of forest formations. TANSLEY believes that this view has not been generally accepted in Europe or in America, and feels that the universal dominance of climatic factors as determinants of climax vegetation has not been proved.

NICHOLS (6) recognized this and returned to SCHIMPER'S distinction between climatic and edaphic formations. His unit next above the association was the edaphic, later called the physiographic formation, which he defined as the association-complex occupying a physiographic unit area, while the climatic formation was a complex of physiographic formations forming the vegetation, taken in its entirety, of any region in which the essential climatic relations are similar or uniform throughout. This TANSLEY criticized, because "nothing like a sharp line can be drawn between one climatic region and another, so that it becomes impossible to delimit climatic formations in NICHOLS' sense." TANSLEY accepts CLEMENTS' "associes" for all stages which have not reached a relatively stable (climax) condition, and defines the association as a mature quasi-organism which is relatively fixed and stable. He then defines the formation as including "all the vegetation which is naturally grouped around the association, determined by the particular collection of environmental factors which make up the ecological conception of the habitat." NICHOLS has not published as yet any further statement on the formation, but in his paper at the Toronto meeting he seems to adhere to his division of formations as physiographic and climatic.

As a result of a study of literature on formations, as well as actual conditions in the field, especially in connection with the preparation of the present paper, the writer has reached the following conclusions, on which the definitions of the terms involved will be based.

1. That there is a distinct advantage in omitting from the definition of the formation all reference to the habitat, as was done in the case of the association.

2. That it is inadvisable to connect the idea of the formation with a climax association, because the determination of climax is one of the purposes of a genetical study, and it is clearly undesirable to define a term which should be usable from the beginning of a study in such a way that it cannot properly be used until the study has been completed. In such a case it would be necessary to secure an additional term for the community in the process of development. This is cumbersome and unsatisfactory, as is illustrated in CLEMENTS' use of "associes" and "association," which does not

seem to meet with general approval in this country at least. In this case there is the additional objection that the more familiar and convenient term is restricted in use to a minority of cases.

3. That the double aspect, abstract and concrete, approved for the association be recognized also for the formation. The abstract concept of the formation, indicated by the use of the definite article, would thus correspond with the Brussels Congress description, and would constitute the formation abstract as a sort of ecological species. The formation concrete might then be regarded simply as any association complex, characterized by a dominant association but including all adjacent associations, whether mature or immature, and other more or less anomalous or unidentified communities connected with them. Thus the formation concrete in general would correspond to NICHOLS' physiographic formation, although the habitat is omitted from the definition, and contiguity made the basis on which the communities are united in the formation. Individual formations may be named either from the dominant association or from the physiographic nature of the area occupied.

4. If a unit above the formation is desired, it will be found convenient to associate the formations of a region in a larger group, which NICHOLS (6), following SCHIMPER, has characterized as a climatic formation. TANSLEY has demonstrated the inadvisability of the term, but the fact remains that the concept is a convenient one, especially for field use, and the writer suggests that the term "formation complex," or simply "complex," be used for this concept. If it be objected that complex is equally applicable to lower grades of units, and is actually in use with them, a special term, such as "aggregate," might be employed. It does not seem advisable to use the term formation, even if qualified by a descriptive adjective, for two classes of units of different grade. Indeed this concept may be identified sufficiently by general expressions already in use, such as vegetation, formations, or even forest (as in "vegetation of Connecticut," "formations of the Great Lakes region," "temperate deciduous forest," etc.).

On the whole, it seems advisable to follow TANSLEY and NICHOLS in emphasizing the vegetational content of the community and regarding the habitat as the sum total of the environmental factors,

and therefore not employing it to indicate any definite portion of the surface of the earth. There is an advantage in employing a special term for the ground occupied by each synecological unit, and the writer tentatively uses the word "locality" for the ground occupied by an individual association, "area" [1] for that occupied by a formation, and "region" for that occupied by a formation complex.

The present study is to be regarded as a preliminary reconnoissance rather than as a completed work. Its purpose is to indicate the lines along which such a study should proceed, and to suggest some tentative conclusions. It is the intention of the writer to make a thorough study of the morphology and physiology of these communities, and in the light of those results to review the tentative conclusions now reached. This preliminary survey will also serve to introduce the region to ecologists, and to show the unusual opportunity for the study of the very diverse communities of a region in relatively primitive condition. Incidentally the writer regards the region as one which should be included in a list of regions to be preserved in their natural condition.

Description of habitat

GEOGRAPHY.—The region is located in Benzie County, Michigan, and adjoins on the north the Crystal Lake Bar region already reported (10). It may be described as a right-angled triangle whose base is about eight miles long, extending south-southeast from a point on the shore of Lake Michigan about two miles northeast of Point Betsie, almost to the town of Honor on Platte River. The east side of the region is the perpendicular of the triangle, and extends north from Honor nearly to the town of Empire on Lake Michigan. The shore forms the hypothenuse, curving slightly to the south with a projection at the mouth of Platte River. It has a total area of about twenty-five square miles, of which perhaps one-fifth is occupied by lakes and ponds. The region is locally known as the Platte Plains, although it is composed of sand ridges and hills, and the general relief is distinctly rolling rather than flat (fig. 1).

The Lake Michigan shore is bordered by a strip of moving dunes ranging from 200 to 500 yards wide. As the prevailing winds are

[1] This is an ecological use of the term, and differs materially from its floristic use.

from the southwest, this dune strip has been protected by the morainic ridge (fig. 2) north of Point Betsie, and the dunes are relatively low and do not have the scenic features to be found in similar areas elsewhere. South of the narrow belt of moving dunes are found the sand ridges, roughly parallel with the shore, with intervening depressions, some still containing small ponds. These ponds occur almost exclusively in the portion of the region west of Platte

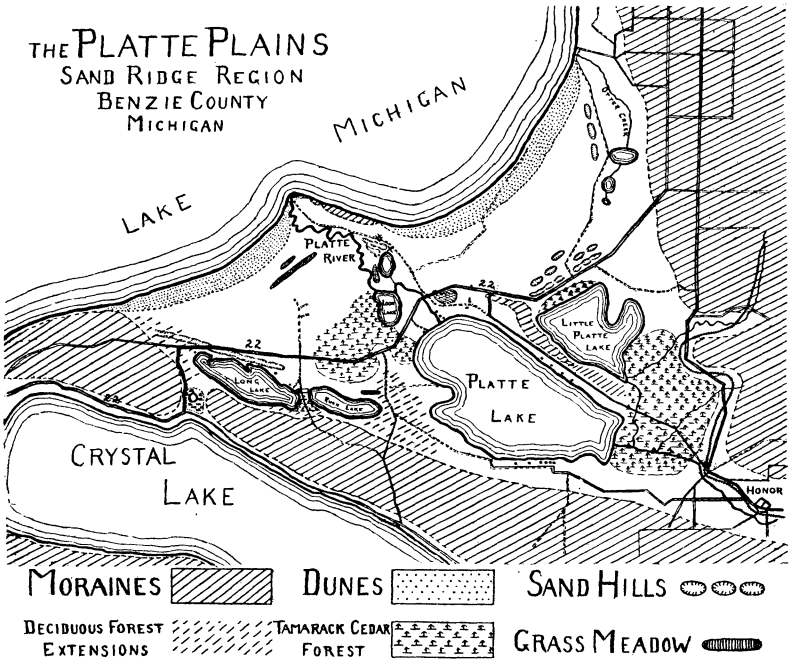

FIG. 1.—Map of Platte Plains sand ridge region

River, probably because of the protection of the morainic ridge which has prevented them from being filled by blown sand. Between the sand ridges lies a wide trough of relatively slight depth, which contains a series of six lakes, more or less completely connected and draining into the Platte River, and three small lakes draining to the north through Otter Creek.

GEOLOGY.—This region is regarded as having been a shallow embayment of Lake Algonquin, whose shores were formed by

morainic uplands. The shore line of the embayment is clearly traceable along the southern and eastern border of the Platte Plains as shown on the map. On the west the old shore line, protected by the morainic ridge, is marked by low rounded knolls, but on the south and east it still shows the characteristics of a wave-formed bluff (fig. 3). This feature has been continued by wave action in the lakes on the south, and it is especially marked on the east, where it borders the floodplain of Otter Creek (fig. 7). There it still remains as a steep bank rising 150 or 200 feet above the plains. The present

FIG. 2.—View toward southwest over shore dunes to morainic ridge which formed the Algonquin shore on the south.

sand ridges with intervening depressions were formed originally as sand bars by the receding waters of Lake Algonquin, assisted by the winds, which piled dunes of varying heights up to 100 feet above Lake Michigan on the successive beaches left bare by the receding lake. One morainic fragment is found on the present shore line half a mile east of the mouth of Platte River, in shape like a hogback, with a very steep forested slope on the south and an equally steep bluff of erosion facing the lake (fig. 10). The line of hills between Platte Lake and Little Platte is a morainic remnant exactly in line with the fragment on the shore. Morainic gravel has been found

in at least one spot midway between the two; so it seems probable that these represent the remains of a moraine which originally bisected the triangle, and which later determined the location of Platte River.

ENVIRONMENTAL CONDITIONS.—The factors of the environment are similar to those of the Crystal Lake Bar region (10), and will not be repeated here. A study of the soil acidity by WHERRY'S method is planned for the near future, and will probably yield interesting results. The variations in soil and moisture content are evidently

FIG. 3.—View toward the southwest over Platte Lakes, showing Algonquin shore line in distance.

of great importance. The substratum consists in the main of beach and dune sand, but there is a mixture of morainic material around the edges where moraine clay and gravel were washed down by the waves of Lake Algonquin and by atmospheric agencies since that time. The materials of the low morainic ridge which bisect the area are also of considerable importance, and their significance will be considered in connection with the migration of the deciduous forest elements into the sand ridge vegetation.

While the slight moisture content of the superficial layer of sandy soil is generally recognized, it has been thought that the

moister conditions of lower layers and the low wilting coefficient of sand would prevent a serious deficiency of moisture for plants adapted to that habitat. The very dry weather in the first part of the summer of 1921, however, apparently caused serious results, although the full effects of these conditions cannot yet be determined. The leaves of the blueberries and other small shrubs dried up early, and while the plants were not killed, their vegetative development for the following summer was greatly reduced. A number of oak and pine seedlings up to two feet in height were evidently killed.

FIG. 4.—Typical sand ridge vegetation, with *Pteris aquilina* in center

Similar "red summers" were reported by the farmers as having occurred at intervals of eight or ten years. It is evident that they would profoundly affect the development of a dense growth of trees on these ridges. Various fires, chiefly prehistoric, have also had an influence. The areas which were affected by these fires should be determined and mapped, and their influence on the present vegetation more definitely determined.

Morphology and distribution of communities

MOVING DUNE FORMATION.—The dune vegetation is practically the same as that of the Point Betsie dune complex already described

(10, 11), with the important exception that there are numerous groves of *Pinus Banksiana* occupying depressions just back of the foredune, and apparently originating in pannes.

SAND RIDGE FORMATION.—The sand ridge area was originally covered by a forest of pine and oak whose trees had reached considerable size. This forest had been burned before the white settlers came to the region. Many of the dead trees were cut while still standing, and many of their stumps still remain. A few patches were not burned, perhaps being protected by neighboring bodies of water, and these give some idea of what the original forest might have been (fig. 8). Reproduction has been good all over the region, and with fifty years' growth behind it, the forest might be regarded as half-way to maturity. While strictly this region should be regarded as a secondary succession, most of the area has practically been untouched by man, and the development seems to be well on its way toward a reproduction of its original condition, so that with the aid of apparently untouched portions it should be possible to work out the stages of the original succession.

The trees of this formation in the order of their importance are *Pinus Strobus*, *P. resinosa*, *P. Banksiana*, *Quercus ellipsoidalis*, *Q. alba*, *Q. rubra* (*Q. velutina* apparently should belong here, but has not been certainly identified), *Acer rubrum*, *Betula alba papyrifera*, *Populus tremuloides*, *P. grandidentata*, *Amelanchier canadensis*, and *Prunus pennsylvanica*. The shrubs found on the sand ridges are *Cornus stolonifera* near the dune belt and *Rhus typhina* farther south (fig. 4). In the undergrowth are found *Pteris aquilina*, *Gaultheria procumbens*, *Vaccinium vacillans*, *V. pennsylvanicum*, *Melampyrum americanum*, and *Ceanothus virginiana*, with *Cladonia rangiferina*, several cushion mosses, and occasionally *Selaginella rupestris* in the drier portions. In the more mesophytic spots occur also *Pedicularis canadensis*, *Galium* sp., *Maianthemum canadense*, *Diervilla Diervilla*, and *Aster cordifolius*. Near the dunes are found *Artemisia canadensis*, *Smilacina stellata*, *Arctostaphylos uva-ursi*, *Apocynum cannabinum*, *Rosa blanda*, *Juniperus communis*, and *J. horizontalis*.

ASSOCIATIONS OF SAND RIDGE DEPRESSIONS.—The depressions between sand ridges are small oval bowls or pockets averaging only a few hundred yards in greatest length. They show all types of

aquatic communities, from those which are nearly all floating aquatics to the grass meadow or the swamp shrub thicket. There are few characterized by a true bog mat, but many contain characteristic bog plants and shrubs. The grass meadows vary in size from a few yards in diameter to one 100 yards wide, and one-half to three-quarters of a mile long; while two others of equal length are 200–300 yards wide (fig. 11). These are usually bordered by a narrow shrub zone between the sand ridge and the meadow, including *Alnus incana*, *Pyrus arbutifolia*, *Rosa carolina*, and *Cornus stol-*

FIG. 5.—*Chamaedaphne* meadow with *Picea Mariana* and *Larix laricina*

onifera. With the grasses and sedges in the smaller meadows are found also *Hypericum virginicum* and *Spiraea salicifolia*, while occasional specimens of aquatics occur, as *Iris* and *Sagittaria*. In one case a remarkable growth of *Lobelia cardinalis* covered one acre of meadow with its scarlet flowers.

The bogs are generally found at or near the border of a lake or river, and are of two general types, one an ericad heath, the other a tamarack thicket. The heath type has a more or less continuous cover of sphagnum with its usual accompaniments: *Sarracenia purpurea*, *Vaccinium macrocarpon*, *Drosera rotundifolia*, *Menyanthes*

trifoliata, *Aspidium Thelypteris*, and in the wetter portions *Typha latifolia*, *Iris versicolor*, and *Phragmites communis* (fig. 5). The shrubs are *Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Vaccinium corymbosum*, *Betula pumila*, and rarely *Ledum groenlandicum*. The trees if any are scattered, and include *Larix laricina*, *Picea mariana*, and where the substratum is very dry *Pinus resinosa* and *P. Strobus*.

The bogs of the thicket type are covered with a dense growth of *Larix* with some *Thuja occidentalis*, mingled with shrubs of *Alnus*

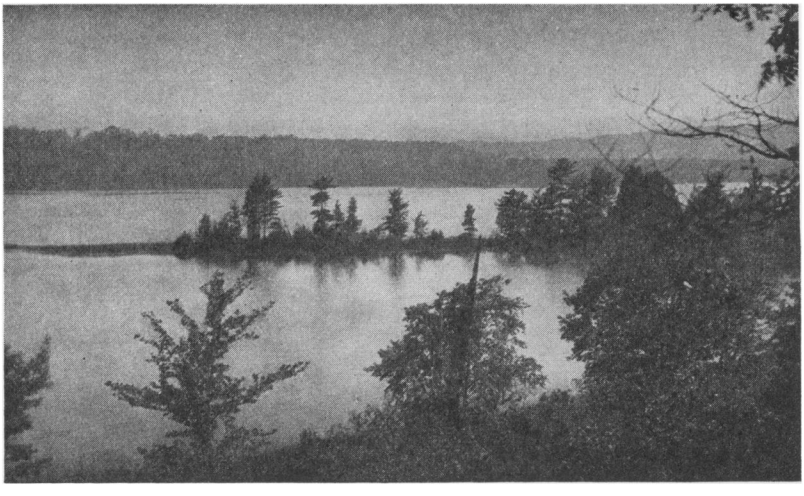

FIG. 6.—Long Lake, with pines on sandy point; Algonquin shore line in distance

incana, *Betula pumila*, *Rosa carolina*, *Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Cornus stolonifera*, *Eupatorium perfoliatum*, *Myrica Gale*, and occasional specimens of *Cypripedium* sp. These thickets are usually surrounded by a zone of *Thuja*, sometimes narrow but occasionally of sufficient area and maturity of trees to be called a "cedar swamp." Here are found in addition *Fraxinus americana*, *Betula alba*, *Abies balsamea*, and *Acer rubrum*. Around the outer edges next the sand ridge, small specimens of *Tsuga canadensis* are locally found.

In the cedar forests the shade is very heavy. The roots of the trees interlace above the water or semiliquid muck, while the under-

growth grows on the peaty soil which has collected in hummocks or on the layer of tree roots. Shade-tolerant mosses are abundant, and occasional restricted patches of sphagnum occur. Among flowering plants the most common are *Coptis trifolia, Cornus canadensis, Trientalis americana, Maianthemum canadense, Aralia nudicaulis, Gaultheria procumbens, Viola* spp., and occasionally *Clintonia borealis. Aspidium spinulosum* and *Osmunda regalis* are frequently found, and some *Taxus canadensis.*

FIG. 7.—Algonquin shore, kept steep by erosion of Otter Creek

VEGETATION OF RIVER AND LAKE BORDERS.—In the Platte Plains there are no true alluvial floodplains, and the shores of streams and bodies of water are either rather steep sandy slopes, or else shallow bays or lagoons inhabited by one of the types of communities already described (figs. 6, 12). The lakes are frequently shallow some distance from shore, and these shallows generally contain extensive colonies of *Scirpus.* There is usually a fringe of aquatic plants, including *Typha latifolia, Sparganium, Sagittaria, Scirpus,* etc., or of shrubs including *Myrica Gale* and *Decodon verticillatus.* On flowing streams the latter does not seem to advance from year to year, probably on account of being torn away by ice in the spring. In

this region *Decodon* is chiefly confined to streams, as it has been observed on lakes or ponds in only one or two instances.

VEGETATION OF MORAINIC UPLANDS.—The morainic uplands were covered with a typical climax beech-maple-hemlock forest, which has been sufficiently described elsewhere (**10, 12**). In some places this is almost untouched, and in at least two places, near Lake Michigan on the west and south of Long and Rush Lakes, the tension zone between it and the sand ridge vegetation is in practically its original condition. In the first locality this zone is about a quarter of a mile wide, and its elements mingle with those of the sand ridge formation. On the south it descends the steep Algonquin terrace to the shores of Long Lake, and merges with the cedar forest between Long and Rush Lakes, and south and east of Platte and Little Platte Lakes (fig. 7). North of Little Platte it originally stopped on the crest of the steep bluff which borders the Otter Creek valley, and the bluff was occupied by a xerophytic conifer association, of which only a few patches now remain.

Development of communities

As already stated, the purpose of genetic synecology is to indicate the successional relationships of the communities of a region, and the place of each in a developmental series. In the present study there is no rock substratum present, and only a very restricted amount of clay or gravel, so that the communities found are largely confined to the psammosere and the hydrosere. Secondary successions are present, both in burned areas and to a limited degree in clearings, but in the present paper the chief concern will be to trace the stages of the original succession (prisere). With one or two minor exceptions the influence of climatic and physiographic factors is so slight as to be negligible, and the region is so young geologically that there seems to be no necessity for the consideration of paleoecological relationships.

SAND SUCCESSION (PSAMMOSERE)

PIONEER STAGES.—*Xerarch.*—The pioneer stages of this succession are confined to the strip of shifting sand along the lake. The initial vegetation includes *Ammophila arenaria* as the absolute

pioneer, associated with *Artemisia caudata*, *Calamovilfa longifolia*, *Cirsium Pitcheri*, *Campanula rotundifolia*, *Cakile maritima*, *Lathyrus maritima*, *Prunus pumila*, *Salix longifolia*, *S. syrticola*, *Senecio vulgaris*, *Solidago* spp., *Aster* sp., *Zygadenus chlorantha*, *Hudsonia tomentosa*, *Arctostaphylos uva-ursi*, *Juniperus communis*, and *J. horizontalis*. All of these are able to germinate on dune sand, but only *Ammophila* is able to become established in pure sand. The others are stunted and soon die, unless their roots come in contact with buried plant material, from which apparently they are able to obtain the necessary mineral elements. *Ammophila* and perhaps *Calamovilfa* are the only plants which cover the ground thickly enough to act as stabilizers. The other herbaceous plants are also scattered, and never grow close enough to form a ground cover in the moving dune belt. *Arctostaphylos* and *Juniperus horizontalis* germinate occasionally on the open sand, but it is doubtful whether they can stabilize. Whenever they occur in sufficient quantity to cover the ground, it is usually by invasion from a patch already established.

Hydrarch.—*Juncus balticus* and willows are the usual pioneers in pannes. Occasionally a local patch of *Pinus Banksiana*, with more or less *Thuja occidentalis*, *Abies balsamea*, and *Betula alba*, forms a clump or grove, which may reach the size of several acres and spread over small valleys or local patches of level sand. There is no evidence of any extensive permanent stabilization by coniferous trees in the belt of moving sand next to the lake. They frequently occur as narrow strips or tongues between advancing lee slopes. The transition from this area to the pine-oak ridges is very marked as one crosses the irregular line of crescent-shaped lee slopes and comes to the lower rounded ridges, where the force of the wind is much less marked and the plants of the pine-oak stage have become established. From this it would appear that the coniferous tree stage originates in pannes, but does not really become widespread so as to form a forest into which the more mesophytic pines and oaks gradually migrate and become dominant, but that the coniferous patches are relatively scattered, and their only influence is as humus formers and as centers of distribution for certain elements of the pine-oak stage. Stabilization, therefore, is due to a diminu-

tion of the force of the wind, either on account of the increasing distance from the shore as the lake waters recede, or by the building up by the wind of high dunes which form a windbreak and protect the sand ridges.

PINE-OAK STAGE.—With the relative cessation of sand movement, coupled with increase of humus, the pine-oak stages begin. As might be expected, the content of vegetation on the ridges shows a certain amount of progressive change, both in floristic content and in the density of growth and mesophytism, as we traverse the

FIG. 8.—Grove of old pine, oak, and hemlock, probably protected by proximity to Platte River.

region from the vicinity of the lake toward the south (that is, from younger to older ridges). On the first ridges there is a preponderance of conifers and many relics of the herbaceous pioneers, especially *Artemisia*, *Smilacina stellata*, *Arctostaphylos*, and *Juniperus* spp. The first tree of this stage to come into the coniferous association of the open dunes is *Pinus Strobus*, followed shortly by *P. resinosa*. *Quercus ellipsoidalis*, *Q. alba*, and possibly *Q. velutina* follow rather slowly, and now may be found fairly evenly distributed in the more advanced portions of the area. *Acer rubrum* is very frequently met near Platte River, or in other somewhat moist

localities. *Betula alba*, *Populus grandidentata*, and *P. tremuloides* are fairly common all through the region. As has been stated, the region has been burned probably more than once, although fortunately not in recent years. The extent of area covered by any one burning is uncertain. Certain local differences in distribution can best be explained on the assumption that the burnings have not been very complete; certainly some patches which bear old pines and hemlocks must have escaped (fig. 8), but patches of white birch and poplars indicate a secondary succession after fires.

FIG. 9.—Luxuriant growth of *Pteris aquilina* in mesophytic habitat, second growth birch and poplar in background.

The undergrowth varies from the modified pioneer type of the ridges nearest the lake to a mesophytic type containing many forms belonging to the climax beech-maple-hemlock forest. These mesophytic associations are not distributed in accordance with the geologic age of the ridges, but are determined rather by edaphic conditions. They will be considered in the section on the beech-maple-hemlock invasion. In addition to the typical mixed ground cover already described, there are two types of undergrowth societies unevenly distributed over the ridges, an almost pure *Pteris aquilina* society and a *Vaccinium* society including *V. penn-*

sylvanicum, *V. vacillans*, with considerable *Gaylussacia baccata*. On the whole, the *Pteris* communities are more characteristic of the portion of the ridge area west of the Platte River and the *Vaccinium* of that east of the river. No definite factors determining the distribution of these communities have yet been established. The *Pteris* seems to be more moisture-requiring than the *Vaccinium*, and it certainly grows more luxuriantly in the moister habitats (fig. 9). The *Vaccinium* species are usually regarded as more acid-tolerant, and investigations along these lines may yield definite results.

BEECH-MAPLE-HEMLOCK STAGE.—It is generally recognized throughout Michigan that the deciduous hardwood forest is confined to rich clay or loamy soil, white pine forests are found on sandy loam, and the pioneer conifers on poor sandy soil. The development of a climax deciduous forest on fixed dunes, as found in the Point Betsie region and at other points along the Michigan shore, is an interesting problem, the solution of which should materially be aided by the evidence to be obtained from a study of this relatively untouched region. As suggested by the preceding morphological study, the climax forest which developed on the morainic upland has begun to invade the sand ridge area along all lines of contact between the moraines and the sand, the undergrowth having gone farthest, and the tree species migrating more slowly. The first tree of the climax forest to appear in the sand ridges is *Tsuga canadensis*, scattered specimens of which are found up to a quarter or half a mile from the morainic border in the tension zone on the west, and for varying distances on the other borders of the sand ridge area. Many parts of the lowland border on the south have been cleared of trees, but in the small triangle between Long and Rush Lakes the deciduous forest is in contact with a cedar swamp, and we can find there a horizontal succession in practically untouched condition. The first hardwood pioneers in the swamp are *Fraxinus americana*, *F. nigra*, *Ulmus americana*, *Tilia americana*, and *Acer rubrum*. As *Thuja* disappears, the trees of the beech-maple-hemlock forest begin to come in on an alluvial substratum, forming a lake plain washed down from the Algonquin

terrace on the south. The largest trees have been cut, but hemlock stumps up to four feet in diameter are still to be seen.

On the strip of land between Long and Platte Lakes a scattered and somewhat stunted growth of *Tsuga canadensis*, *Acer saccharum*, and *Fagus americana* extends north almost to Michigan Highway 22, over soil which at first is somewhat alluvial, but which gradually changes into the usual sand ridge type. Toward the north the hard maples disappear first and the hemlocks last, as the oaks and pines become more frequent. On the east very little uniform advancement of the deciduous trees was found, probably because of the steep xerophytic bluff occupied by conifers (fig. 7). The valley of Otter Creek has not been studied in detail as yet, but it seems to be largely occupied by conifers, although the soil conditions are more those of an alluvial floodplain than in any other part of the sand ridge region.

Apart from this rather uniform invasion along the borders, there are several isolated spots where hemlocks at least are found in some frequency and of considerable size. On the morainic ridge between Platte and Little Platte Lakes the deciduous forest was apparently well developed, with, however, a large proportion of pines and some oaks. Large hemlocks are found in several places along the east bank of Platte River north of Platte Lake (fig. 8), and in the valley on the south slope of the morainic fragment on the shore of Lake Michigan (fig. 10). In the last locality they are in poor condition, and some have recently died. Small specimens are to be found on the edges of many of the smaller swamp depressions, especially on the southwest of Loon Lake, that is, on the opposite side of Platte River from the morainic ridge extension just mentioned. *Fagus americana* has not been found away from the borders and the wedge-shaped invasion between Platte and Little Platte Lakes. A solitary specimen apparently about fifty years of age is growing by Michigan Highway 22, about a quarter of a mile west of Platte River, and therefore in the heart of the sand ridge area. Its shape shows that it grew in the open, but its age does not preclude the possibility of its having been planted by the first settlers. The mixed coniferous-deciduous lake bluff border association described

in the Crystal Lake Bar region (10) does not appear in this region, probably because the corresponding habitat is not present. This association contained *Thuja occidentalis*, *Abies balsamea*, *Tilia americana*, and *Ostrya virginiana*, mixed with the trees of the climax deciduous forest on the crest of the bluffs facing Lake Michigan. It was apparently due to the exposure to sun and lake winds, combined with low soil moisture content. The only place where it might have been expected was on the high bank at the eastern edge of the

FIG. 10.—Morainic remnant on shore of Lake Michigan; landward slope equally steep, with hemlocks growing in valley.

sand ridge region, and there the only conifers seem to have been *Pinus Strobus* and *P. resinosa*.

The preceding discussion indicates that the migration of the beech-maple-hemlock forest into the sand ridge formation has been of two sorts, one a general advance along all lines of contact between the two formations, the other in a long slender belt on the morainic ridge and its remains, to the shore of Lake Michigan (fig. 10). Unpublished investigations by the writer indicate that for the establishment of *Thuja occidentalis* and *Abies balsamea* on sandy soil it is necessary that there should be present in the sand enough moisture to carry the young tree root below the drought zone. This

may be held by humus in the soil, or by a high moisture content in sand relatively free from humus, and it seeems possible that this may also be true for *Tsuga*, but not for *Fagus*. *Acer saccharum* seemed to hold an intermediate position between the two, and its apparent absence from any advanced positions on the sand ridge habitat was a distinct surprise. Morainic soil equally with humus seems to afford a suitable substratum for the establishment of all the species mentioned, either because of the supply of necessary mineral elements, or because these minerals make possible a better utilization of the water present. For these reasons the advancement of the deciduous formation seems to be the result of increased humus content and mesophytism, and also a pushing forward by sheer force of numbers. The parent seed trees being so near at hand and supplying so many seeds, it follows that in time a fair number of seedlings have been able to find conditions favorable to growth and so become established. In the other case, the morainic substratum affords a soil peculiarly favorable to the deciduous trees, and while a much smaller number of seeds have lodged on it, a relatively larger proportion have become established. In view of the fact that the shade and moisture conditions vary greatly on different parts of this ridge, it would seem to be the chemical constituents of the soil which give to it its favorable characteristics.

The question may be raised as to whether this condition may not be the result of the prehistoric fires, previous to which the beech-maple-hemlock elements may have been more widely distributed, and the present isolated groups may be relics preserved because of the protection of bodies of water. Against this view may be set the evidence of tradition and the entire absence of stumps in other moist habitats of the region which seem to have been untouched by fires. Unquestionably even hemlock stumps and logs do not last as long as pine, but it might be expected that some traces would remain if they had been at all widespread in comparatively recent times. This, however, would not account for the appearance of hemlocks on the edges of swamps at some distance from these relic patches. It is also reasonable to suppose that reforestation after a fire would proceed along general lines similar to those of

the original advance, so that in either event the stages of the prisere would be approximately as outlined.

AQUATIC SUCCESSION (HYDROSERE)

The substratum in this succession is standing water, either in closed depressions such as ponds and small lakes, or in open depressions as bays or lagoons along the banks of lakes or of Platte River. These various bodies of water show practically the same vegetation for the first three stages, commonly designated as the *Potamogeton*, *Nymphaea*, and *Scirpus* stages. After that different lines of succession are found, depending on the condition of the habitat.

SAND RIDGE DEPRESSIONS CONTAINING STANDING WATER.—In these depressions the water is fairly shallow, but the depression is surrounded by sand ridges whose slopes rise directly from the water's edge. Here are to be found either swamp or bog stages according to the condition of the substratum. In the swamp type the fourth stage is a narrow sedge zone, the shrub growth is scanty, mostly willows, and the sand ridge vegetation descends the slopes almost to the water's edge. In the bog type the quaking mat is seldom found, but there is a dense growth of sedges and grasses on a fairly solid muck foundation. This contains such bog plants as *Menyanthes trifoliata*, *Potentilla palustris*, and occasionally *Sarracenia purpurea*, and *Sphagnum* sp. The shrub zone is a dense thicket of *Alnus incana*, *Pyrus arbutifolia*, with some *Hamamelis virginiana*, and sometimes with scattered specimens of *Thuja occidentalis* and even *Tsuga canadensis* mingling with poplars and the first trees of the pine-oak association. The water is frequently shallow on the north side of the pond, possibly from sand blown in by the winds from Lake Michigan, and of course is exposed to the heat of the sun, but protected from the colder winds. The south side has deeper water, and is more sheltered from the heat of the sun on account of the shade of the pines and oaks, but exposed to the cold winds. In depressions of this kind the swamp vegetation is found on the shallow, warmer, northern side, while the bog type occurs on the deeper, cooler, southern side. In depressions which are sheltered on all sides and in which the water is deep all over, the bog type generally prevails over the whole pond.

GRASS MEADOW TYPE.—Here the fourth stage is one dominated by grasses and sedges forming a relatively solid turf. In the smallest depressions the sedge society may be only a few yards square, and in it there are often found swamp plants such as *Hypericum virginicum*, *Spiraea salicifolia*, and *Rosa carolina*, as well as occasional relics of the aquatic stages. The later stages resemble those of the swamp type already described. The larger grass meadows are relatively limited in number, only four or five having been discovered so far, and they have certain peculiar features which seem to demand special consideration. The first is the mature condition of the extensive grass turf, and the other is the absence of any tendency of the shrubs and trees to invade the meadow. Where the grass meadow is surrounded by a shrub zone of the swamp type, this may be accounted for on the assumption that the depression was originally all very shallow, thus favoring a development of turf so rapid that the shrubs and trees had no chance to become established before the mat of grass roots had completely occupied the substratum. There are, however, some features which indicate that the grass mat was formed recently and very rapidly, indicating perhaps a physiographic change in comparatively recent times. These are best shown in a grass meadow visited only once, as it was discovered in a hurried reconnoissance trip, and so far there has been no opportunity for a second visit. This meadow is located just west of the lower reaches of the Platte River very near the strip of moving dunes on the shore. It extends from northeast to southwest practically in a straight line for rather more than half a mile, but is less than a hundred yards wide at the point crossed, although somewhat wider to the east and the west. At this point there were imbedded in the grass on both edges of the meadow trunks of dead trees extending out from both banks, and on each tree was growing a row of tamaracks apparently not over twenty-five years old. There were scattered tamarack trees on the lower edges of the sand ridges. While the localization of the tamaracks on the dead logs and not in the grass is not surprising, the preservation of the logs long enough for the grass turf to form and the apparent youth of the trees makes a very interesting problem. This meadow apparently has never been mowed or burned. The

logs may have come from trees killed by prehistoric fires, as they had no bark on them, but they were not charred, and otherwise seemed well preserved, with many dead branches extending up among the young tamarack trees. In fact, the whole situation suggested the sudden freezing of the surface of a pond, solidifying into a green grass mat, instead of a covering of ice. In the case of the large meadow occupying a shallow swale between Long and Rush Lakes, which at one time might have been a water connection between the two lakes, the shore showed the regular horizontal

FIG. 11.—Grass meadow near Long Lake; bog shrubs on left, with tamaracks and cedar swamp behind them.

stages of a bog-cedar forest succession, but the center of the swale is occupied by a meadow with solid turf (fig. 11). The meadow has been mowed for years, and was recently ditched for draining, but this treatment apparently has not changed the general relations. The shrub zone at its southern edge is the usual bog shrub stage, followed by a belt of tamaracks of considerable size. A mature cedar forest adjoins this on the south, with a fairly dry substratum and some of the undergrowth elements of the deciduous forest. Next come deciduous swamp trees, and finally the trees of the climax forest. Here we have a bog forest left high and relatively dry, with a grass meadow formed at its edge.

Each of these formations, although differently situated (one in the heart of the sand ridges, the other between two lakes), seems to indicate the same physiographic change, that is, a sudden lowering of the water table by several feet. This change might be referred to the activities of the first white settlers about fifty years ago. The Long Lake area is very close to Crystal Lake, and might have been partially drained by seepage when Crystal Lake level was lowered in 1871 (10). A low terrace on the south bank of Long Lake adds weight to this hypothesis. The other meadow must have come very close to Platte River at its eastern extremity, and may have been lowered in connection with the first lumbering operations at about the same time.

Another explanation of the lowering of the water is based on diastrophic changes. Observations on the shore of Lake Michigan, both on the Michigan side and on the Green Bay Peninsula opposite, indicate that fifty years ago the lake was several feet higher than the highest levels of recent years, and this fall of level might have affected the level of Platte River in its lower reaches (fig. 12). There are also extensive meadows bordering Platte River and the sluggish stream connecting Platte and Little Platte Lakes, whose origin may be connected with the lowering of water levels at about the same time. Further study, both of the floristic content and of the nature of the substratum, is necessary before definite conclusions can be reached. There is no indication of any migration of trees into a grass meadow with solid grass mat, whether large or small, but there seems to be some evidence that they can come in on a floating mat of the swamp type. Further investigation may show that the latter case is really a bog mat, in which event it would not be available as evidence, and the presence of trees would be quite in accordance with the rule for bog mats.

Bog type.—Here the fourth stage develops as a bog mat composed of sphagnum and the usual accompanying bog plants. In several cases this has developed into an ericad heath composed largely of *Chamaedaphne*, *Andromeda*, occasionally *Ledum* and similar shrubs, including *Betula pumila*, and scattered trees of *Larix*, *Picea mariana*, and occasionally *Pinus Strobus* and *P. resinosa*. In other cases the tamaracks with some bog shrubs and

Thuja have come in very thickly, forming a bog thicket which in some cases apparently may develop into a cedar forest. The tamaracks in this region are all small, with the exception of those between the shrub belt and the cedar forest already noted between Long and Platte Lakes. The occurrence of bog vegetation in the depressions among sand ridges has already been noted. The variation in depth on opposite sides also applies to some extent to the larger ponds and lakes. In the latter cases the shallow portions are characterized by extensive *Scirpus* colonies, but the bog asso-

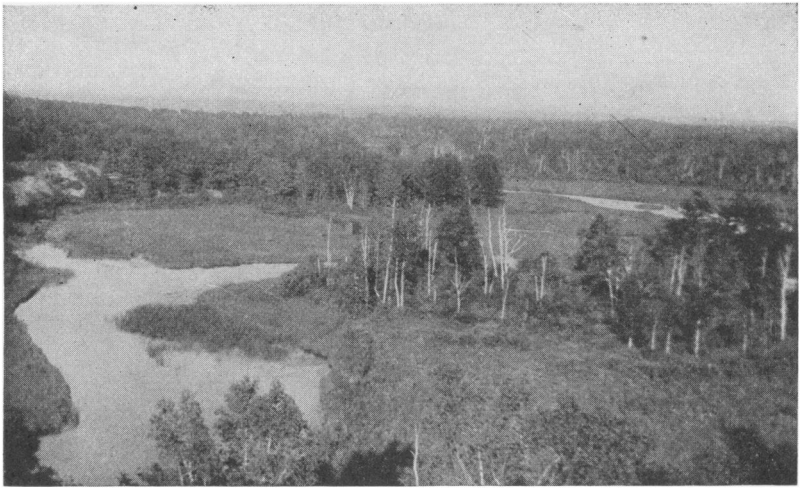

FIG. 12.—Lower reaches of Platte River, bordered by grass meadows, with some second growth birches; sand ridges in distance.

ciations do not appear along the shores of the lakes. In open bays and lagoons there was no general uniformity, but swamp or bog types were found corresponding to the varying local conditions. From this it is concluded that the development of the later stages of the hydrosere into the swamp or the bog type is dependent chiefly on depth of water and temperature. Investigations as to acidity have not been made as yet, but it is assumed that here, as elsewhere, the swamp type will be associated with a neutral or alkaline condition and the bog type with high acidity. The tree stage in the hydrosere was found to follow only the quaking mat

stage, and not the grass meadow. If we accept the hypothesis for the very recent formation of the large grass meadows, the absence of trees might be attributed to shortness of time, but the same condition is found in the smallest meadows, which from their position and general appearance must be regarded as contemporaneous with the wet depressions and with the sand ridges themselves, and here there should have been ample time for invasion. It does not follow necessarily that the grass meadow is an edaphic climax, but it is evident that that association will remain stable for a very long time. As already noted, the bog mat passes relatively rapidly into a tamarack cedar forest, which quickly receives hydrophytic deciduous elements, and thus passes into the climax deciduous forest.

Summary

1. Genetic synecology is that part of ecology which deals with the developmental relations of plant communities. In a limited region the development of successions (seres) is definitely related to the character of the substratum. In this region two such seres are found, the sand succession (psammosere) and the aquatic succession (hydrosere). The clay-gravel succession (geosere) has reached its climax on the surrounding moraines, and is observed only as it invades the sand ridge region.

2. In this study the successional units, the concrete association and formation, are defined as follows. The association is a plant community of essentially uniform (or homogeneous) physiognomy and ecological structure, and of essentially uniform (or homogeneous) floristic composition as regards dominant species. The formation is an association-complex characterized by a dominant association, but including all adjacent associations, whether mature or immature, and other more or less anomalous or unidentified communities associated with them. The unit above the formation is a formation complex, or aggregate, and is composed of the formations of a definite region which may be limited by climatic or geographic boundaries. The ground occupied by an association is called a locality, that occupied by a formation an area, and that occupied by a formation complex a region.

3. The vegetation of the region studied is found to be a formation complex consisting of a sand dune formation, a sand ridge

formation, and swamp and bog formations. It occupies a region which consists of sand ridges with depressions containing bodies of water of all sizes, from a few yards to a mile or more in diameter. Geologically the region was a shallow bay of Lake Algonquin drained by the recession of the waters of the lake with the melting of the ice barrier in the Straits of Mackinaw.

4. The first stages of the sand succession (psammosere) are found in the moving dune belt along the shore, but they do not lead to a complete stabilization of the sand. The later stages appear when the sand stops moving as a result of a checking of the force of the wind, due to distance from the shore or the formation of high dunes which act as windbreaks. The pine-oak stage shows a progressive change from the less mature areas near the lake to the more mesophytic areas in the southern portion of the region. Soil moisture content and the amount of humus in the sand seem to be important factors in this change.

5. The clay-gravel succession (geosere) has reached the climax stage as a beech-maple-hemlock forest on the surrounding morainic upland, and is found invading the pine-oak formation along the borders of the region, and especially along a narrow morainic tongue which extends completely through the sand ridge substratum to Lake Michigan. The controlling factor in this invasion seems to be primarily the chemical character of the soil, glacial material ranking close to humus in importance, and secondarily the soil moisture content.

6. The various ponds and lakes all show the normal early stages of the aquatic succession (hydrosere), which lead either to swamp meadows or to bog forests, the line of development followed being determined chiefly by depth of water and exposure to the heat of the sun.

NORTHWESTERN UNIVERSITY
EVANSTON, ILL.

LITERATURE CITED

1. CLEMENTS, F. E., Plant succession. Carnegie Publ. no. 242. 1916.
2. COOPER, W. S., The climax forest of Isle Royale, Lake Superior, and its development. BOT. GAZ. **55**: 1–44. 1913.

3. COWLES, H. C., The physiographic ecology of Chicago and vicinity, a study of the origin, development, and classification of plant societies. BOT. GAZ. **31**:73–108; 145–182. 1901.
4. ———, The causes of vegetative cycles. BOT. GAZ. **51**:161–183. 1911.
5. MOSS, C. E., Geographical distribution of vegetation in Somerset. Royal Geog. Soc. 1907.
6. NICHOLS, G. E., The interpretation and application of certain terms and concepts in the ecological classification of plant communities. Plant World **20**:305–319; 341–353. 1917.
7. ———, Abstract in printed program of Ecological Society of America for Meeting at Toronto, December, 1921.
8. TANSLEY, A. G., Types of British vegetation. Cambridge. 1911.
9. ———, The classification of vegetation and the concept of development. Jour. Ecology **8**:118–149. 1920.
10. WATERMAN, W. G., Ecology of Crystal Lake Bar region. Ann. Report Mich. Acad. Sci. **19**:197–208. 1917.
11. ———, Development of root systems under dune conditions. BOT. GAZ. **68**:22–53. 1919.
12. WHITFORD, H. N., The genetic development of the forests of Northern Michigan. BOT. GAZ. **31**:289–325. 1901.